

Chapter 6

Predicting Primate Behavior from Personality Ratings

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Abstract An important reason for measuring personality in any species is the determination of the predictive power between personality ratings and manifest behavior. In this chapter, I review what is known to date about the relationships between personality traits and overt behaviors in primates. The majority of studies that have found such links have done so at the factor level, so I also present new data from my own research with chimpanzees, gorillas and bonobos, where I test for relationships between specific trait terms and observed behavior within the broader overall dimensions (factors) of personality, along with associations between these factor scores and behaviors. Principal components analysis of chimpanzee personality ratings yielded six components accounting for 77.5% of the variance in ratings. Demonstrating convergent and discriminant validity, I illustrate links between factor scores on the top three factors (each accounting for more than 15% of the variance) concerned with Confidence (C1), Sociability (C2) and Excitability (C3), and behaviors – e.g., Sociability (C2) scores correlate positively with several observed play indices. Examples of behaviors linked to discrete trait adjectives include significant correlations between rated playfulness and aggression and their respective observed behavioral frequencies. In addition, some relationships are specific to particular age or sex classes – e.g., the relationships between *confidence* and *effectiveness* and increased grooming are only evident among male chimpanzees, while immature individuals scoring higher on *intelligent* engage in more grooming. I also present preliminary findings of relationships between personality ratings and observed behaviors for the smaller samples of gorillas and bonobos. That the behavioral data here correlate significantly with both specific traits and with factor scores provides validation of the rating instrument and will benefit our understanding of nonhuman personality.

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6.1 Introduction: Personality and Behavior

Personality is a fascinating aspect of the psychological life of any individual, whether human or nonhuman. Invariably, when we hear the term “personality,” we want to gain an insight into the inner world of a particular individual and a big part of that involves how they behave. What are they likely to do? Will they be nice to me? Will I be better than them? Answering such questions depends largely on our ability to demonstrate clear and valid relationships between personality traits and the way individuals overtly behave.

A growing body of nonhuman research now helps us see interesting links between personality variables and behavior. In this chapter, I will review research validating personality trait ratings with manifest behavior among primates.

Personality traits can be defined as lasting dispositions which lead to characteristic behavior across situations, with different individuals reacting in different ways to the same situation (e.g., Cervone and Pervin 2008). If behavior is influenced by personality, the ability to measure personality should facilitate prediction of behavior. The early use of human personality tests as diagnostic tools (e.g., in personnel selection) did not, however, always allow such prediction, leading to criticism of the entire concept of traits (Mischel 1968). As the situation alone is equally wanting in allowing the prediction of behavior (Funder and Ozer 1983), the optimal approach is an interactionist one, taking account of both situational factors and personality traits. The more specifically defined the personality trait is, the more likely it is that behavior will be consistent across the relevant situations, although individuals also vary in the extent of consistency on particular traits, and in the extent of predictability across situations (Klirs and Revelle 1986).

6.2 Surveying the Literature

I began by carrying out systematic searches of the relevant databases (PsychINFO, Web of Science) using the terms “personality” and “temperament” (which are still often used interchangeably) and behavior, and searching for key names in the primate order as well as the more generic “ape,” “monkey” and “primates” (after Gosling 2001; Jones and Gosling 2005). Studies that had subjective as well as behavioral measures of the same personality traits were targeted. Some article titles included both “temperament” and “behavior” but did not use any rating scale for example, individual differences in temperament do not just reflect behavioral and emotional characteristics, but have also been explored in relation to brain and physiological functioning (e.g., Kalin et al. 1998). A study of cortisol reactivity in tufted capuchins (Byrne and Suomi 2002) is an example of looking at personality and behavior in relation to one or more additional variables, often physiological or immunological measures.

Closer inspection of the abstracts and/or method and results sections showed that many studies included aspects of either personality or behavior – or both – but did

not correlate separate personality ratings and behavioral codings. Examples of this include Fairbanks (2001), in which an index of social impulsivity was derived from a behavioral factor analysis, and Weiss et al. (2002) in which dominance was not measured separately as a behavioral coding but as an additional factor on the rating scale. I did not include dominance as a behavior as studies exploring links between personality and dominance often involve computation of other variables and/or subjective impressions of dominance rank. For example, Buirski et al. (1978) reported links between subjective dominance rank and Emotions Profile Index (EPI) personality traits such as *aggressive* and *distrustful* in chimpanzees. Following an iterative process, the references of relevant articles were scanned for new research not already identified. Results are shown in Table 6.1.

Table 6.1 shows that studies have focused entirely on apes and Old World monkeys, especially the Cercopithecines. Konečná et al.'s (2008) recent study was the first to examine personality in the Colobines and to use a Five-Factor Model (FFM)-based questionnaire on a monkey species. Sufficient detail about the sample is reported in most studies and some researchers have focused purely on males (Capitanio 1999, 2002; Kuhar et al. 2006; Konečná et al. 2008).

More studies report validation of factor scores (rather than traits) with observed behavior, while some report links between behaviors and both specific traits and factor scores (e.g., Stevenson-Hinde et al. 1980a; Murray 1995). Some researchers (Pederson et al. 2005; Konečná et al. 2008) do the opposite and present two types of behavior coding with factor scores: specific behaviors and those behaviors categorized into social contexts or components.

The focus of this review is on studies using trait rating scales of one type or another – arguably the only way to measure personality in nonhumans. The growing body of literature suggests that the trait paradigm to measure primate personality is psychometrically robust (e.g., Gosling 2001). However, interrater reliability is more often reported than is validity.

Another important methodological consideration is the independence of the trait ratings and behavioral observations and codings. This is not always reported clearly, but often these are done simultaneously by the same researcher(s), although if one researcher conducts the behavioral observations and also contributes to the personality ratings but other multiple raters are also involved and a high level of interrater reliability is demonstrated, the situation is improved. Arguably, it is optimal to have the ratings completed by one team of researchers and the behavioral codings by a separate team (e.g., Capitanio 1999; Pederson et al. 2005). In this way, if there is repetition in terms of behavioral definitions for trait terms, each set of raters and observers is only conceptualizing that description once and independently of each other. Capitanio's (1999) study did not only include independent ratings and observations but also incorporated a longitudinal element showing that personality factors predicted behavior up to 4.5 years later, as well as demonstrating that their predictive power is cross-situational.

Table 6.1 shows many examples of convergent validity between personality ratings and overt behaviors that would be predicted if they are both expressing the same latent variable; for example, sociability, playfulness, or aggression.

Table 6.1 Summary of research validating nonhuman primate personality ratings with observed behavior

Species/study	n ^a	Factor/trait/other	Behavior
<i>Chimpanzees</i>			
Buirski and Plutchik (1991) ^b	1	aggressive (+) depressed (+) distrustful (+) trustful (–) timid (–) controlled (–) gregarious (–)	Infanticide, cannibalism
Murray (1995) ^d	59	Confidence	Males’ grooming rate (+) Males’ rate being groomed (+) Males’ % significant groomers (+) Males’ % significant partners groomed (+) Immatures’ responsibility for proximity (+) Rate of play (+) % significant play partners (+) % time spent alone (–) Responsibility as groomee (+) Males’ display rate (–) Males’ responsibility as groomer (+) Immatures’ rate being groomed (+) Immatures’ % significant groomers (+) Immatures’ aggression rate (–)
		Sociability	Rate of grooming (+) Median association time (–) Rate of aggression (+) Adults’ rate being groomed (+) Adults’ rate of play (+) Adults’ % significant partners (–) Immatures’ % time spent alone (+) Immatures’ display rate (+)
		Excitability	
Lilienfeld et al. (1999) ^c	34	<i>Chimpanzee Psychopathy Measure Score</i>	Play wrestling and tickling performed and received (+) Play chasing performed and received (+) Repetitive movement (–) Detachment (–) Gentle teasing received (–) Low-intensity agonism received (+)
King and Landau (2003)	49	Subjective well-being	Submissive Context Behaviors (–) Submissive avoidance (–)

(continued)

Table 6.1 (continued)

Species/study	<i>n</i> ^a	Factor/trait/ <i>other</i>	Behavior
Pederson et al. (2005)	49	Dominance	Submissive-watch (–) Aggressive display (+) Submissive Context Behaviors (–) Agonistic Context Behaviors (+)
		Extraversion	Idle (–) Public orientation-watch and greet (–) Gymnastics (+) Cling (+) Affiliative approach (+) Affinitive Context Behaviors (+) Public Orientation Context Behaviors (–)
		Dependability	Aggressive display (–) Agonistic Context Behaviors (–)
		Agreeableness	Aggressive display (–) Groom (+) Agonistic Context Behaviors (–)
		Emotionality	Aggressive display (+) Scratch (–) Agonistic Context Behaviors (+)
		Openness	Idle (–)
Vazire et al. (2007) ^c	52	aggressive	Contact-infant (–) Solitary play (–)
		belligerent, irritable dominant	Threat (+) Contact-infant (–) Solitary play (–) Object manipulation (–) Self-groom (+)
		eccentric depressed	Repetitive (+) Social play (–) Solitary play (–) Object manipulation (–)
		friendly, sociable	Social play (+) Contact-infant (+) Solitary play (+)
		solitary solitary, sullen	Flee (–) Social play (–) Contact-infant (–) Solitary play (–) Object manipulation (–)
		active	Groom received (–) Contact-infant (+) Solitary play (+) Object manipulation (+)
		playful	Flee (+) Avoid (+)

(continued)

Table 6.1 (continued)

Species/study	<i>n</i> ^a	Factor/trait/other	Behavior
			Social play (+) Contact-infant (+) Solitary play (+) Object manipulation (+) Locomotion (+)
<i>Bonobos</i>			
Murray (1995)	4	active, excitable, fearful, insecure playful, sociable playful curious effective, popular deferential sociable fearful, insecure slow	Responsibility for play (–) Responsibility for play (+) Rate of play (+) Rate of grooming (+) % significant partners groomed (+) % significant partners groomed (–) % time spent alone (–) % time spent alone (+) Rate of aggression (+)
<i>Gorilla</i>			
Murray (1995)	13	tense active confident, effective, irritable deferential slow, solitary sociable	Rate of aggression (+) Females' display rate (+) Immatures' % significant groomers (+) Immatures' % significant groomers (–) Immatures' rate being groomed (–) Immatures' rate of play (–)
Kuhar et al. (2006)	25 M	Extraverted Dominant Fearful Understanding	Initiate affiliative behaviors (+) Receive affiliative behaviors (+) Initiate contact aggression (+) Initiate displacements (+) Receive displacements (–) Initiate displacements (–) Initiate noncontact aggression (–)
<i>Great apes</i>			
Uher and Asendorpf (2008) ^e	20 A	friendly to youngsters persistent physically active sexually active	Friendliness to youngsters Persistence Physical activity Sexual activity
<i>Olive baboons</i>			
Buirski et al. (1973) ^f	7	<i>Protection</i> (less fearful) <i>Deprivation</i> (more sullen, jealous) <i>Rejection</i> (more defiant, belligerent) <i>Destruction</i> (more aggressive)	Mean time being groomed (–) Mean time being groomed (+) Mean time being groomed (+) Mean time being groomed (+)

(continued)

Table 6.1 (continued)

Species/study	<i>n</i> ^a	Factor/trait/other	Behavior
<i>Vervet monkeys</i>			
McGuire et al. (1994) ^g	86	Social competence	Solitary (–) Submit (–) Vigilance (+) Groom (+) Aggression (+)
		Playful/curious	Solitary (–) Active (+) Play (+) Explore (+)
		Opportunistic	Active (+) Aggressive (+)
<i>Hanuman langurs</i>			
Konečná et al. (2008)	27 AM	Agreeableness	Aggression (contacts vs. threats) (–) Displacement rate (–) Aggression rate (–) Touch penis (+) Grooming time (+) H'partners approaching (Shannon index) (+)
		Confidence	Dominance component behaviors (–) Aggression (close vs. distant) (–) Terminate groom (–) Locomotion (–) Grunt and grimace (+) Display (+) Displacement rate (+) Copulation (+) Passive affiliation time (+) Approach rate (+) Dominance component behaviors (+) Involvement component behaviors (+) Activity component behaviors (–)
		Extraversion	Synchronization/rest (–) Resting time (–) Terminate groom (+) Activity component behaviors (+)
<i>Rhesus macaques</i>			
Stevenson-Hinde et al. (1980a)	N/A	aggressive effective	Hits, threats and chases (+) Displacement of/Avoidance by others (+)
		excitable	Displays/threats directed outside cage (+)
		fearful	Fear grins and avoidance of others (+)
		playful	Playful behavior (+)
		sociable	Total number of contact partners (+)

(continued)

Table 6.1 (continued)

Species/study	<i>n</i> ^a	Factor/trait/other	Behavior
Stevenson-Hinde et al. (1980b)	N/A	Confident	Mothers had infants that initiated contact and play with others, and did not maintain close proximity to their mothers One year olds maintain proximity to and initiate play with others and had experienced high rejection rate by mother at weaning age (16 weeks)
		Excitable	Mothers initiated close contact with infants, that did not maintain close proximity to others One year olds had high rate of mother-initiated close contact and restraint at 8 weeks
		Sociable	Mothers had infants that initiated contact with others One year olds had initiated contact with others at 8 weeks
	N/A	Confident	Infant males' latency to touch a banana in a Strange Situation test (+) Male response to novel mirror (gaze/lipsacks) (–) Infant females' time to complete reinforcement test (+)
		Excitable	Infant males' time spent in test cage when novel ball present (+) Infant males' frequency of whoop calls in test (–) Infant males' time to complete reinforcement test (–) Infant males' time spent holding lever in slide test (+)
		Sociable	Infant males' activity in test (–) Infant females' time to complete reinforcement test (+) Infant males' time spent holding lever in slide test (+)
	33	Sociability	Approaches initiated and received in natal group (+)
		AM	Fear grimace initiate in natal group (–) Beginning of group formation: Threat initiate (–) Fear grimace receive (–) Approach receive (+) Proximity duration (+)

(continued)

Table 6.1 (continued)

Species/study	<i>n</i> ^a	Factor/trait/ <i>other</i>	Behavior
			Nonsocial duration (–)
			Once group established:
			Fear grimace initiate (–)
			Approach initiate (+) and receive (+)
			Groom present initiate (+) and receive (+)
			Proximity duration (+)
			Nonsocial duration (–)
			Groom duration (+)
			Phase 1 dyad formation:
			Groom present initiate (+) and receive (+)
			Duration groom initiate (+)
			Lipsmack receive (+)
			Fear grimace receive (–)
			Sex present receive (+)
			Grunt receive (+)
			Proximity duration (+)
			Nonsocial duration (–)
			Phase 2 dyad formation:
			Sex present initiate (+) and receive (+)
			Grunt initiate (+) and receive (+)
			Duration groom initiate (+) and receive (+)
			Lipsmack receive (+)
			Fear grimace receive (–)
			Yawn receive (–)
			Groom present receive (+)
			Proximity duration (+)
			Nonsocial duration (–)
		Confidence	Groom receive in natal group (+)
			Fear grimace receive in natal group (+)
			Sex present receive in natal group (+)
			Beginning of group formation:
			Lipsmack initiate (–)
			Sex present receive (–)
			Fear grimace initiate (+)
			Once group established:
			Approach initiate (–) and receive (–)
			Phase 1 dyad formation:
			Lipsmack initiate (–) and receive (–)
			Grunt initiate (–) and receive (–)
			Sex present receive (–)

(continued)

Table 6.1 (continued)

Species/study	<i>n</i> ^a	Factor/trait/other	Behavior
			Duration groom receive (–)
			Proximity duration (–)
			Nonsocial duration (+)
			Phase 2 dyad formation:
			Groom present initiate (+) and receive (–)
			Grunt initiate (–) and receive (–)
			Duration groom initiate (–) and receive (–)
			Lipsmack receive (–)
			Fear grimace receive (+)
			Sex present receive (–)
			Nonsocial duration (+)
		Excitability	Displacements initiated and received in natal group (+)
			Fear grimace initiate in natal group (+)
			Chase initiate in natal group (+)
			Sex present receive in natal group (+)
			Aggression initiate in natal group (–)
			Approach/contact receive in natal group (–)
			Groom receive in natal group (+)
			Response to threatening human:
			Back of cage location (–)
			Threat initiate (+)
			Beginning of group formation:
			Threat initiate (+)
			Lipsmack initiate (–)
			Fear grimace initiate (+) and receive (+)
			Sex present initiate (+) and receive (–)
			Groom present receive (–)
			Proximity duration (–)
			Nonsocial duration (+)
			Groom duration (–)
			Once group established:
			Fear grimace initiate (+) and receive (–)
			Approach receive (–)
			Nonsocial duration (+)
			Groom duration (–)
			Phase 1 dyad formation:
			Lipsmack initiate (+)

(continued)

Table 6.1 (continued)

Species/study	<i>n</i> ^a	Factor/trait/other	Behavior
Capitanio (2002)	12 AM	Equability	Fear grimace initiate (+) and receive (+)
			Sex present initiate (+)
			Duration groom receive (–)
			Phase 2 dyad formation:
			Lipsmack initiate (+)
			Grunt initiate (–)
			Fear grimace receive (+)
			Nonsocial duration (–)
			Approach initiate in natal group (–)
			Threat receive in natal group (+)
			Beginning of group formation:
			Approach initiate (–) and receive (–)
			Groom present initiate (–) and receive (–)
			Sex present receive (–)
			Proximity duration (–)
			Nonsocial duration (+)
			Groom duration (–)
			Once group established:
			Threat initiate (–)
			Groom present initiate (–) and receive (–)
			Phase 1 dyad formation:
			Fear grimace receive (–)
			Groom present receive (–)
			Grunt receive (+)
			Duration groom receive (–)
			Phase 2 dyad formation:
			Grunt initiate (–) and receive (+)
			Groom present receive (+)
			Duration groom receive (–)
			Proximity duration (+)
“Sit and stare” response to video playback: yawn (+), watching (+), activity (–) during social stimulus; lipsmack (–) during nonsocial stimulus			
Higher latency to avert gaze from screen			
<i>Stump-tailed macaques</i>			
Mondragón-Ceballos and Santillán- Doherty (1994)	27	Confident	Evasive (–) Copulatory (+) Feeding (–) Bizarre (–)

(continued)

Table 6.1 (continued)

Species/study	<i>n</i> ^a	Factor/trait/other	Behavior
		Sociable	Submissive (+) Amiable (+) Self-grooming (–) Resting (–)
		Excitable	Threatening (+) Rambling (+) Bizarre (+)
Santillán-Doherty et al. (2006)	22	Novelty-seeking	Risk-taking Curiosity

^a*N* is given only where clearly stated in the study. Samples are of mixed sex/age composition, unless indicated as *M* males; *F* females; *A* adults; *I* immatures

^bReports links between trait rating individual differences and subsequent unusual behavior, but behavior codings were not carried out concurrently with trait ratings

^cOnly correlations reaching $p < 0.01$ level of significance are reported here

^dCorrelations shown here are between personality factors and behaviors. For correlations between personality traits and behaviors, see details in chapter

^eStudy pooled 5 of each of the following species into a Great Ape sample: orangutans, bonobos, chimpanzees, gorillas. Significant correlations ($p < 0.01$) between adjective ratings and behavior measures are given here – see Uher and Asendorpf (2008) for correlations between behavior measures and “behavior ratings”

^fUsed Emotions Profile Index (EPI): protection, deprivation, rejection and destruction are emotions derived from scores on the traits defiant, assertive, submissive, obedient, belligerent, impulsive, alarmed, cautious, jealous and sullen; $n = 7$; $p < 0.05$

^gFive of the eight behaviors observed in this study were not independent, as they were also included in the personality assessment as coded observed behaviors and were included in the factor analysis which generated the personality factors

^hOnly partial correlation coefficients greater than 0.25 are reported here. See Capitanio (1999) for descriptions of behavioral responses to specific video stimuli

6.2.1 Personality Trait Level Relationships with Behavior

In examining the relationships between behavior and specific personality traits, we can see that ratings on *playful* correlate positively with observed play behavior in chimpanzees (Vazire et al. 2007; Murray 1995 – see Table 6.2), bonobos (Murray 1995), and rhesus macaques (Stevenson-Hinde et al. 1980a). *Aggressive* ratings also correlate positively with overt aggression in chimpanzees (Murray 1995) and rhesus macaques (Stevenson-Hinde et al. 1980a), while rates of aggression correlate positively with ratings on *tense* in gorillas and *slow* in bonobos (Murray 1995). Higher ratings on the trait *sociable* are related to increased play behavior in chimpanzees (Vazire et al. 2007; Murray 1995). More *sociable* bonobos also initiate more play and spend less time alone (Murray 1995), while *sociable* rhesus macaques have more contact partners (Stevenson-Hinde et al. 1980a) and *sociable* chimpanzees have been found to increase contact with infants (Vazire et al. 2007).

The report by Buirski and Plutchik (1991), albeit involving only one adult female chimpanzee, illustrates a relationship between an unusual profile of personality

Table 6.2 Validated predictions of correlations between adjectives and behaviors among chimpanzees

Adjective	Behavior	All	<i>M</i>	<i>I</i>
Active	Rate of play	0.45		
Aggressive	Rate of aggression	0.42		
Confident	Rate being groomed ^a		0.72	
	Rate of grooming ^a		0.66	
Curious	Rate of play	0.44		
Deferential	% Significant groomers ^a		−0.68	
Effective	% Significant groomers ^a		0.69	
Fearful	% Significant partners groomed ^a		−0.66	
Irritable	Rate of grooming	0.44		
Playful	Rate of play	0.79		
	Responsibility for play	0.43		
	% Significant play partners	0.64		
Popular	% Time spent alone	−0.50		
	Rate of play	0.48		
	% Significant play partners	0.44		
	Rate being groomed ^a		0.65	
Protective	Rate being groomed	0.41		
	Rate of grooming	0.41		
Slow	Rate of play	−0.54		
Sociable	Rate of play	0.53		
	Responsibility for play	0.41		
	% Significant play partners ^a			−0.67
Solitary	% Time spent alone	0.44		
	Rate of play	−0.63		
	% Significant play partners	−0.56		
	Responsibility as groomee	−0.41		
Strong	Rate of displays	0.48		

Correlations significant at $p < 0.001$ ($n = 59$)^a Prediction validated among males or immatures only

ratings on the EPI and subsequent deviant behavior, involving the adult, Passion, and her daughter, Pom, who infamously killed and consumed several infants from their own community. There is, however, a retrospective aspect to this study as the authors were prompted to reexamine the ratings in light of the horrific behavior, rather than having made predictions at the time of the ratings; thus, the EPI instrument's diagnostic and predictive power may be overstated. The only other nonhuman primate study relating EPI ratings to behaviors showed a link in baboons between the amount of grooming received and individuals rated as less *fearful* (emotion dimension: Protection), and more *sullen*, *jealous* (Deprivation), *defiant*, *belligerent* (Rejection) and *aggressive* (Destruction) (Buirski et al. 1973).

Using an adapted version of the Stevenson-Hinde et al. (1980a) rating scale, I found that adult chimpanzees with higher ratings on *protective* received more grooming, while, using yet another instrument, Vazire et al. (2007) found an inverse relationship between grooming received and *sullen* in chimpanzees. These complicated

findings illustrate some of the difficulties in interpreting and attempting to compare findings across studies. Not only are the species different, but so are the rating scales and sometimes the meanings of the same word: in the EPI, Protection is used as a label for Fearfulness (and presumably the need or desire for protection) whereas it would mean more or less the opposite in the scale I used.

With personality traits often being behaviorally defined, critics may argue that semantic similarity leads to somewhat obvious links between traits and behaviors, and there is a potential for circularity:

Q: Why is Boris playful?

A: Because he has a high rating on the adjective *playful*.

Q: How did he get that rating?

A: I filled out a questionnaire that defined *playful* as “plays a lot.”

This is an extreme example (and not based on an actual definition from an existing questionnaire) but this objection could not be leveled at all adjectives as they do not have such clear-cut semantic similarity (e.g., *sullen*, *apprehensive*, *tense*). Even the adjective *sociable* is complex as it could potentially relate to a multitude of predictable behaviors, much as an underlying dimension of personality does. Pederson et al. (2005) suggest that such narrow trait ratings may be useful as they are easier to obtain than behavioral observations; however, to make such ratings, one needs to spend extended periods of time becoming acquainted with each rated individual. Nevertheless, once completed, a set of personality scores is an excellent way of gaining a quick snapshot impression of an individual and a potentially useful tool for decision-makers in charge of animal husbandry and welfare.

One way that researchers have tried to overcome some of the above criticisms is to use factor scores rather than (or in addition to) trait ratings. Objections due to semantic similarity and circularity cannot be so easily made if it is many or several of these traits that contribute in precise and meaningful ways to underlying global dimensions of personality.

6.2.2 Personality Factor Level Relationships with Behavior

Table 6.1 shows that Extraversion is positively linked to affiliative or affiliative behaviors in chimpanzees (Pederson et al. 2005) and gorillas (Kuhar et al. 2006), while Sociability relates positively to play behavior in chimpanzees (Murray 1995), affiliative behavior in rhesus macaques (Capitanio 1999), and amiable yet submissive behavior in stump-tailed macaques (Mondragón-Ceballos and Santillán-Doherty 1994). Excitability appears to be related to more grooming behavior in both rhesus macaques (Capitanio 1999) and chimpanzees (Murray 1995) but the relationship with aggressive behavior is different between these species, with more Excitable chimpanzees having a higher aggression rate while rhesus macaques higher on Excitability initiate less aggression. In stump-tailed macaques, Excitable scores correlate positively with behavior described as threatening, rambling, and bizarre (Mondragón-Ceballos and Santillán-Doherty 1994).

Personality ratings of rhesus macaque mothers have also been found to correlate with ratings of their infants throughout the infants' first year of life; for example, infants of highly Confident and Sociable mothers initiate more contact with other group members (Stevenson-Hinde et al. 1980a).

Confident scores correlate with increased grooming in chimpanzee (Murray 1995) and rhesus macaque (Capitanio 1999) males, and have also been found to relate to more copulatory behavior in langurs (Konečná et al. 2008) and rhesus (Capitanio 1999) and stump-tailed (Mondragón-Ceballos and Santillán-Doherty 1994) macaques. Some of the more surprising findings for more Confident primates include a decrease in aggression in langurs (Konečná et al. 2008) and a higher latency to touch a banana in a strange situation test in rhesus macaques (Stevenson-Hinde et al. 1980b).

Pederson et al. (2005) reported that chimpanzees' scores on personality dimensions are associated with behavior in particular contexts; for example, Dominance and Emotionality scores relate positively to agonistic behaviors. Scores on the Dominance factor correlate negatively with predictable submissive behaviors in chimpanzees (Pederson et al. 2005) and with displacements received by gorillas (Kuhar et al. 2006), and submissive context behaviors in turn are shown to relate inversely to chimpanzees' scores on a Subjective Well-Being scale (King and Landau 2003). In addition, scores on a comparable Social Competence factor relate negatively to submissive behavior in vervet monkeys (McGuire et al. 1994). A suite of behaviors constituting a Dominance behavioral component inversely relate to the Agreeableness factor in Hanuman langurs (Konečná et al. 2008). Individuals higher on Agreeableness spend more time grooming and this holds true for these langurs, as well as for chimpanzees (Pederson et al. 2005).

6.3 Elucidation of Personality-Behavior Relationships at Two Levels in an African Ape Study

Previously, I have combined analyses of individual chimpanzees' ratings on adjectives with the effects of situational influences such as grouping and rearing (Murray 1998), and of individual characteristics such as age and sex (Murray 2002), to determine the impact of these factors on personality. In this section, I will illustrate how both discrete personality trait ratings and personality factor scores relate to observed behavior in a sample of 59 chimpanzees from three UK zoos: a social group of 22 at Chester Zoo, another social group of 11 at London Zoo, and 26 individuals housed in groups, pairs or trios at Twycross Zoo. They ranged in age from 19 months to 45 years and contained 39 females and 20 males (see Murray 1995, 1998, 2002 for further details).

Relationships between traits and behaviors will also be examined for smaller samples of gorillas ($n=13$) and bonobos ($n=4$). The gorillas were housed at London and Twycross Zoos, were aged between 20 months and 30 years, and included five males and eight females. The bonobos at Twycross Zoo included one male and three females, aged 3–12 years.

6.3.1 Methods

6.3.1.1 Personality Ratings

I adapted the rating scale used by Stevenson-Hinde with rhesus macaques (Stevenson-Hinde and Zunz 1978; Stevenson-Hinde et al. 1980a), by omitting the item *understanding* and including the item *intelligent*. *Motherly* was changed to *maternal/paternal* and *subordinate* was changed to *deferential*. Zookeepers and I completed the 28-item scale, full details of which have been published previously (Murray 1998, 2002).

6.3.1.2 Reliability

Interrater correlations (Pearson) were examined for each ape individually, and raters were regarded as reliable when their ratings correlated significantly with at least one of the other raters ($p < 0.01$). In fact, 91% of the reliable raters were reliable at the $p < 0.001$ level of significance. Overall, a high percentage of significant interrater correlations were found, with 80% for male chimpanzees and 81% for females. Multiple regression analysis also showed that 83% of the variance in rating was accounted for by individual ape variation, with only 0.2% due to raters, and 16.8% due to raters and adjectives; a strong indication that raters were assessing individual subjects on adjectives differently as well as discriminating effectively between adjectives.

In addition, I computed the reliabilities of the adjectives: significant coefficients ranged from 0.40 for *curious* to 0.84 for *deferential*, with a mean of 0.57. Three of the 28 adjectives – *permissive*, *predictable*, and *sensitive* – were subsequently omitted from further analysis as they failed to reach the required level of significance ($p < 0.001$) when correlation analyses were performed on the ratings of two raters per item across subjects.

6.3.1.3 Correlation and Principal Components Analysis

I calculated mean scores per adjective per individual and Pearson correlation analysis was performed on the data from each of the three species to identify how adjectives related to each other and clustered together. In addition, principal components analysis (PCA) was conducted on the chimpanzee data. Both varimax rotation and the unrotated solution yielded similar results, but I decided to use the unrotated solution, following Stevenson-Hinde and Zunz's (1978) method. Although six factors were extracted in the chimpanzee PCA, together accounting for 77.5% of the variance in chimpanzee personality ratings (see Appendix 1 for the six components which satisfied eigenvalue and scree plot tests), I will here – as previously (Murray 1998, 2002) – focus on the first three: Confidence, Sociability

and Excitability, and relationships between these and other adjectives and behaviors, particularly those concerned with sociability, playfulness, and aggression.

To permit current and future cross-component comparisons, I calculated component (factor) scores for each individual and Spearman correlation analyses were carried out to measure the relationships between both factor scores and personality ratings with the behavioral measures.

As significant sex and age differences in both personality and behavior variables were already established (Murray 1995, 2002), here I conduct within-sex and within-age correlational analyses followed by tests for significant differences between sexes and age groups using Fisher's r to z transformation. Apes up to 107 months are classed as "Immature," and those of 108 months or more are classed as "Adults." Sex and age affect personality and behavior independently, but they will only be discussed here where they have a direct influence on the relationships between personality traits and/or component scores and observed behavior.

6.3.1.4 Behavioral Observations

Over 1,000 h of focal samples of behavior were collected (Altmann 1974), during which I recorded all occurrences of the following behaviors, along with partner preferences, initiator, and terminator where applicable: time spent alone, time spent in association, proximity, grooming, aggression, displays, and playing (see Murray 1995 for further details). Indices of responsibility for proximity, grooming, and play were calculated using the Hinde and Atkinson formula (1970). To allow meaningful comparison between apes, I also summarized the association, proximity, play, and grooming data by calculating percentages of significant partners using a median split.

I made predictions about correlations between particular behavioral measures and adjectives and here present correlations that were validated and those that were not. Additional correlations between ratings and behaviors which had not been predicted are also presented. Some pairings of adjectives are obviously descriptive opposites, such as *active* with *slow*, *confident* and *effective* with *apprehensive/deferential/fearful/insecure*, *aggressive* with *gentle* and *equable*, and, to an extent, *sociable* with *solitary*. Therefore, strong negative correlations were predicted accordingly. Some of the predictions reflect commonsense expectations; for example, that individuals rated more highly on *aggressive* and *playful* would have higher rates of observed aggression and play. The existing literature informed other predictions. Thus, as grooming is cited as a measure of sociability (e.g., Schino 2001, 2007), it was predicted that individuals rated more highly on *sociable* would engage in more grooming activities. Similarly, predictions about grooming were made for those adjectives relating to status and confidence, such that individuals of higher status may both give and receive more grooming (or groom/be groomed by more partners) (Simpson 1973; Goodall 1986), the giving of grooming by more dominant individuals perhaps serving a social bonding or alliance building function (Watts 2000) or acting to reduce tension (Simpson 1973).

6.3.2 *Personality Trait Ratings and Behavior in Chimpanzees*

Tables 6.2–6.4 present correlation coefficients between personality ratings and observed behavioral measures among chimpanzees showing convergent and discriminant validity. It is evident that there is a group of adjectives that strongly relate to a behavioral cluster concerned with play. Broadly, those chimpanzees rated as more playful, in terms of such measures as rates of play, number of play partners and responsibility for initiating play, are more likely to be *active*, *curious*, *playful*, *popular* and *sociable*, and less likely to be the *slower*, more *solitary* individuals. *Solitary* chimpanzees do indeed spend more time alone, while those individuals with higher scores on *strong* also have higher display rates. Similarly, chimpanzees who are rated as more *aggressive* display higher rates of aggression. Grooming rates are positively linked to chimpanzees who are rated as more *protective* and *irritable*.

Among male chimpanzees, there are associations between adjectives relating to *confidence* and *effectiveness* and grooming measures, such that more *confident* males both give and receive more grooming, and those who are rated as more *effective* are groomed by more partners. *Deferential* individuals, on the other hand, are groomed by fewer individuals, while those who are more *fearful*, *insecure* and *apprehensive* groom fewer conspecifics themselves. This could support the reassuring function of grooming whereby the more partners a male chimpanzee grooms, the less *insecure* he is. Similarly, the more minutes per hour a male spends being groomed by another, the more likely he is to be rated as more *confident*.

Grooming measures are often taken as indicators of sociability (e.g., Seyfarth 1977; Goosen 1987; Schino 2001) but, when I included sets of measures related to grooming and to play, I found that more measures relating to play than to grooming correlated highly with ratings on the adjective *sociable*. The only trend between *sociable* ratings and grooming measures is that more *sociable* chimpanzees tend to initiate more grooming (Table 6.3), but they did not give or receive more grooming, nor did they solicit it, and they did not have more grooming partners. Although such assumption of responsibility for grooming could be regarded as an indicator of the role of grooming in social bonding, the relationships between playfulness and sociability are stronger. Apes rated highly on *sociable* play more, have more play partners and, importantly, take more responsibility for initiating play.

One must remember that this could be a result of how the raters decided to rate the animal on that adjective. Despite being given distinct behavioral definitions for each adjective, raters will possibly, to an extent, have their own definition of such words as “sociable” as well as an implicit personality theory regarding which adjectives “go together.” Being sociable may be seen as being fun-loving, active and happy, for instance, which are evident characteristics of playfulness, and therefore raters may be rating apes largely on “playful sociability.” Adding some weight to this possibility, it is noteworthy that these two adjectives load highly positively together on the second component identified for explaining variation in chimpanzee personalities. An alternative explanation could question the reliability of the behavioral

Table 6.3 Predicted correlations not validated among chimpanzees

Adjective	Behavior	Correlation
Aggressive	Rate of displays	0.25
Apprehensive	Rate being groomed	-0.11
	% Significant groomers	-0.18
Confident	% Significant groomers	0.16
	% Significant partners groomed	0.12
	Rate of displays	-0.05
	Rate of aggression	0.20
Deferential	Rate being groomed	-0.11
Effective	Rate being groomed	0.36
	Rate of grooming (M)^a	0.50
	% Significant partners groomed	0.24
	Rate of displays	0.12
	Rate of aggression	0.27
Equable	Rate of aggression	-0.15
	Rate of displays	-0.20
Excitable	Rate of displays	0.37
Fearful	Rate being groomed	-0.09
	% Significant groomers	-0.27
Gentle	Rate of aggression	-0.26
	Rate of displays	-0.28
Insecure	Rate being groomed	0.01
	% Significant groomers	-0.19
Irritable	Rate of aggression	0.27
Maternal/paternal	Rate of aggression	0.68
	Responsibility as groomer (I) ^a	0.26
	Rate of grooming (I) ^a	0.47
	Rate being groomed (M)^a	0.64
	Responsibility for proximity (F)^a	-0.42
	Rate of play (I)^a	0.65
	Responsibility for play (M)^a	-0.65
Playful	% Time spent alone	-0.36
Popular	Median association time	-0.23
	Resp. for proximity (A)^a	-0.42
Protective	Rate of aggression	0.13
	% Significant groomers	0.21
Slow	Rate of grooming	0.25
	Rate being groomed	0.22
	Rate of displays	-0.11
Sociable	Median association time	-0.23
	% Time spent alone	-0.21
	Responsibility for proximity	0.13
	Responsibility as groomer	0.37
	Rate of grooming	0.22
	Rate being groomed	0.10
Solitary	Responsibility for proximity	0.01
	Responsibility for play	-0.38

Correlations not significant $p > 0.001$ ($n = 59$); *bold* denotes $p < 0.05$ ^aCoefficient given for specific age/sex class, which was higher than for all chimpanzees together

Table 6.4 Other significant correlations between ratings and behaviors among chimpanzees not previously predicted

Adjective	Behavior	All	<i>M</i>	<i>A</i>	<i>I</i>
Active	% Significant play partners	0.41			
Aggressive	Responsibility for play	0.48			
	% Time spent alone ^a				0.63
Apprehensive	% Significant partners groomed ^a		−0.68		
Curious	% Significant play partners	0.46			
Excitable	% Time spent alone ^a				0.69
Gentle	Rate of play ^a				0.79
Insecure	% Significant partners groomed ^a		−0.70		
Intelligent	Rate of grooming ^a				0.69
Irritable	Median association time	−0.41			
	Responsibility for proximity ^a				0.64
Playful	Rate of displays ^a		−0.70		
Protective	Responsibility for play ^a			−0.70	
Slow	% Significant play partners	−0.53			
Solitary	Rate of aggression ^a				0.75
	Rate of displays ^a				0.68
Strong	% Time spent alone ^a				0.67
	% Significant play partners	−0.46			
	Rate of play	−0.41			
Tense	% Time spent alone ^a				0.79

Correlations significant at $p < 0.001$ ($n = 59$)^aCorrelation significant among males, adults or immatures only

codings, although play and grooming are arguably two of the easiest behaviors to record, requiring little interpretation.

Table 6.3 shows correlations between adjectives and behaviors that had been predicted, but which were not validated by reaching the required level of significance ($p < 0.001$). Only two of the relationship trends between ratings and behaviors, however, are correlated in a direction opposite to that predicted. In Table 6.4, significant correlations between ratings and behaviors for chimpanzees are shown which had not been predicted previously. Among immature chimpanzees, youngsters who spend more time alone are *stronger*, and more *excitable*, *aggressive* and *tense*, and those rated higher on *solitary* have higher rates of aggression and displays. Interestingly, more *intelligent* immature chimpanzees have higher rates of grooming, possibly emphasizing the ingratiating function of this activity (Goodall 1986).

6.3.3 Personality Trait Ratings and Behavior in Gorillas

Table 6.5 presents significant correlations between ratings and behaviors among gorillas, which are fewer than are present for chimpanzees. There is a strong correlation between being *tense* and a higher rate of aggression, and female gorillas scoring

Table 6.5 Significant correlations between ratings and behaviors among gorillas

Adjective	Behavior	All	<i>F</i>	<i>I</i>
Active	Rate of displays		0.96	
Confident	% Significant groomers ^a			1.00
Deferential	% Significant groomers ^a			-1.00
Effective	% Significant groomers ^a			1.00
Irritable	% Significant groomers ^a			1.00
Slow	Rate being groomed			-1.00
Sociable	Rate of play			-1.00
Solitary	Rate being groomed			-1.00
Tense	Rate of aggression	0.76		

Correlations significant at $p < 0.001$ ($n = 13$); *F* females; *I* immatures^aCorrelations previously predicted**Table 6.6** Predicted correlations between ratings and behaviors among gorillas not significant

Adjective	Behavior	Correlation
Aggressive	Rate of aggression	0.69
Playful	Rate of play	0.67
Sociable	% Time spent alone	-0.24
Solitary	% Time spent alone	0.25

Correlations not significant $p > 0.001$ ($n = 13$); *bold* denotes $p < 0.01$

higher on *active* have higher rates of displays. Confident immature gorillas are groomed by more partners, while their rate of play is inversely correlated with ratings on *sociable*; a surprising finding, and in marked contrast to the positive relationship existing among chimpanzees. Play behavior, like grooming, was relatively rare among gorillas and much of their play was of a more solitary nature, involving running and climbing or playing with objects in their enclosure.

Although not significant, the relationships among gorillas between ratings on *aggressive* and *playful* and their respective observed rates of behavior are nonetheless relatively strong (Table 6.6). Ratings of these apes on *sociable* and *solitary*, however, have no direct relationship with the amount of time spent alone by individuals.

6.3.4 Personality Trait Ratings and Behavior in Bonobos

Several significant correlations ($p < 0.001$) between ratings and behaviors were identified among the small sample of four bonobos. Whereas in chimpanzees, *curiosity* correlates positively with rate of play, among bonobos, it correlates with rate of grooming. The status-related adjectives are, among bonobos, related to partners groomed by, rather than groomers of, the individual (as was the case for male chimpanzees). Thus, *deferential* bonobos groom fewer conspecifics, while *effective* and

popular individuals groom more of their group members. While ratings on *solitary* do not correlate significantly with the amount of time spent alone, as predicted, there is the expected negative correlation between this behavioral measure and *sociable*. Bonobos who spend more time alone are also likely to be more *insecure* and *fearful*. While the predicted correlation between *aggressive* and rate of aggression was not significant, there was the expected correlation between ratings on *playful* and actual rates of play, and more *active*, *excitable*, *fearful* and *insecure* individuals initiate less play, while more *playful* and *sociable* bonobos initiate more play. A positive correlation also exists between ratings on *slow* and rate of aggression.

6.3.5 Summary of Trait–Behavior Correlations

From the above, it is evident that certain adjectives correlate with behavioral measures which one could anticipate, and which therefore confirms the validity of these ratings. These include *aggressive*, *playful*, and *solitary*. For the chimpanzees, Spearman correlation coefficients ranged between 0.41 and 0.79 ($p < 0.001$), which is very similar to the range of trait–behavior correlation coefficients obtained in an earlier macaque study: 0.45–0.73 ($p < 0.001$) (Stevenson-Hinde et al. 1980a).

1. *Active* chimpanzees have higher rates of play and more play partners, while active female gorillas have higher display rates. Active bonobos initiate less play.
2. *Aggressive* chimpanzees have higher rates of aggression and initiate more play. Immature chimpanzees with higher scores on aggressive spend more time alone. The positive correlation between rated and observed aggression is strong but not significant for gorillas and bonobos.
3. *Apprehensive* male chimpanzees groom fewer partners.
4. *Confident* male chimpanzees give and receive more grooming, and confident immature gorillas are groomed by more partners.
5. *Curious* chimpanzees have higher rates of play and more play partners, while curious bonobos engage in more grooming.
6. *Deferential* male chimpanzees and immature gorillas are groomed by fewer others, while deferential bonobos groom fewer partners themselves.
7. *Effective* male chimpanzees and immature gorillas are groomed by more partners, while effective bonobos groom more partners.
8. *Excitable* immature chimpanzees spend more time alone, while excitable bonobos initiate less play.
9. *Fearful* male chimpanzees groom fewer partners, while more fearful bonobos spend more time alone.
10. *Gentle* immature chimpanzees have higher rates of play.
11. *Insecure* male chimpanzees groom fewer partners, while insecure bonobos spend more time alone.

12. *Intelligent* immature chimpanzees engage in more grooming, perhaps as a strategy of ingratiation.
13. *Irritable* chimpanzees spend less time in association with each partner but have higher grooming rates. Irritable immature chimpanzees take more responsibility for proximity to others while irritable immature gorillas receive grooming from more partners.
14. *Playful* chimpanzees have higher rates of play, more play partners, and initiate more play. In addition, playful males have lower display rates. The positive correlation between rated and observed play is also significant for bonobos (who also initiate more play) and is relatively strong for gorillas too.
15. *Popular* chimpanzees spend less time alone and more time playing with more play partners, while popular males receive more grooming. Popular bonobos groom a greater number of partners.
16. *Protective* chimpanzees give and receive more grooming, with the more protective adults initiating less play.
17. *Slow* chimpanzees play less and have fewer play partners, while slower immature gorillas receive less grooming, and slow bonobos have higher rates of aggression.
18. *Sociable* chimpanzees play more and initiate more play, with more sociable immature chimpanzees having more play partners. Sociable immature gorillas, by contrast, play less, while sociable bonobos spend less time alone and initiate more play.
19. *Solitary* chimpanzees spend more time alone, play less, have fewer play partners, and solicit less grooming. Immature chimpanzees who are more solitary have higher rates of aggression and displays, while immature gorillas rated as more solitary receive less grooming. The positive correlation between ratings on Solitary and actually spending more time alone is strong for bonobos, but weak for gorillas.
20. *Strong* chimpanzees display more but play less and have fewer play partners. Immature chimpanzees rated as stronger spend more time alone.
21. *Tense* immature chimpanzees spend more time alone, while gorillas rated as more tense have higher rates of aggression.

6.3.6 *Personality Factor Scores and Behavior in Chimpanzees*

The principal components, or personality dimensions, through which we can better understand chimpanzees are similar to those of Confident to Fearful, Active to Slow and Sociable to Solitary found in rhesus macaques (Stevenson-Hinde and Zunz 1978), and from which Confident, Excitable and Sociable scores were also calculated (Stevenson-Hinde et al. 1980a), and to the Sociability, Confidence, Excitability and Equability components identified in Capitanio's (1999) study with the same species. Some similarities also exist to components labeled Sociable, Dominance, and Anxiety found in stump-tailed macaques (Mondragon-Ceballos et al. 1991), and to those of Socially Competent, Playful/Curious, and Opportunistic found in

vervet monkeys (McGuire et al. 1994). They also bear marked resemblances to the behavioral factors identified for chimpanzees (van Hooff 1970) and rhesus macaques (Chamove et al. 1972). Separate Affinitive and Play motivational systems were identified for chimpanzees, as opposed to the all-encompassing Affectionate/Affiliative/Sociable/Play factor found among rhesus monkeys, but these can all be likened to the Sociability component (C2) in this study. The Fearful and Submissive factors identified for rhesus macaques and chimpanzees, respectively, can also be likened to the Confidence component (C1), and this may equate to the Neuroticism/Stability dimension of human personality. The Hostile/Aggressive factor found in rhesus is more akin to the Excitability component (C3), considered by Chamove et al. (1972) as Psychoticism, but a distinction is made by van Hooff between Aggressive and Excitement for chimpanzees in terms of behavioral counts.

Here, I present the following list of behavioral measures and how they correlate with scores on the components concerned with Confidence (C1), Sociability (C2), and Excitability (C3).

1. *Median association time* – Chimpanzees with higher scores on Excitability (C3) have lower median association times.
2. *% Time spent alone* – The scores of chimpanzees on Sociability (C2) are inversely correlated with the amount of time they spend alone. Among immature chimpanzees, high Excitability (C3) scores are positively associated with greater amounts of time spent alone.
3. *% Significant partners* – Adult chimpanzees with higher scores on Excitability (C3) associate with fewer significant partners.
4. *Responsibility for proximity* – Immature chimpanzees with higher Confidence (C1) scores take more responsibility for proximity.
5. *Rate of grooming* – Chimpanzees with higher scores on Excitability (C3) groom more. Male chimpanzees with high scores on Confidence (C1) have higher rates of grooming.
6. *Rate of being groomed* – Male chimpanzees with higher scores on Confidence (C1) receive more grooming. Immature chimpanzees with high Sociability (C2) scores are groomed at higher rates, while adults higher on Excitability (C3) receive more grooming.
7. *% Significant partners groomed* – Male chimpanzees who score highly on Confidence (C1) groom a greater number of partners.
8. *% Significant groomers* – Male chimpanzees with higher scores on Confidence (C1) also are groomed by more groomers. It is immature chimpanzees with higher scores on Sociability (C2), however, that receive grooming from a greater number of groomers.
9. *Responsibility as groomer* – Male chimpanzees with higher Sociability (C2) scores take more responsibility for initiating grooming.
10. *Responsibility as groomee* – Chimpanzees with higher Sociability (C2) scores solicit more grooming.
11. *Rate of play* – Higher rates of play are evident in chimpanzees who have higher Sociability (C2) scores. Adult chimpanzees with higher Excitability (C3) scores also have higher rates of play.

12. *% Significant play partners* – Chimpanzees with higher scores on Sociability (C2) have more play partners.
13. *Responsibility for play* – No significant findings.
14. *Rate of aggression* – Chimpanzees with higher scores on Excitability (C3) have higher rates of aggression. Immature chimpanzees with higher scores on Sociability (C2), however, have lower rates of aggression.
15. *Rate of displays* – Male chimpanzees with higher Sociability (C2) scores have lower display rates, whereas immature chimpanzees with higher scores on Excitability (C3) display at a higher rate.

These correlation coefficients are comparable to the range of partial correlation coefficients between personality dimensions and a variety of behavioral situations reported by Capitanio (1999), and are relatively higher than the personality dimension and behavior correlations reported for gorillas (Kuhar et al. 2006) and both the dimension-behavioral context and dimension-specific behavior correlations demonstrated by Pederson et al. (2005) for chimpanzees.

6.3.7 Multi-Level Relationships Between Personality and Behavior in Chimpanzees

That measurable individual personalities in captive chimpanzees exist has support from concordance among raters in the quantitative assessment of adjective ratings and from validation of these ratings with observed behavioral measures. This is inconsistent with accusations of ratings being subjective, anthropomorphic, and/or based on the raters' implicit personality theory (see Borkenau 1992 for a review of the controversy). Instead, our descriptions of individuals in their social context are enhanced at more than one level – from examining discrete trait rating patterns to utilizing a more global score on personality dimensions (for a classification of individuals according to personality types based on the pattern of scores representing levels of Confidence, Sociability and Excitability, see Murray 2002, 2005).

Such multi-level assessment of individuals provides information about personality to satisfy differing requirements. Discussing the rationale behind the development of the facet scales within each of the five factors in the NEO-PI-R (Costa and McCrae 1992), the authors state that, "Interpretation on the domain level yields a rapid understanding of the individual; [while] interpretation of specific facet scales gives a more detailed assessment." (Costa and McCrae 1995, p. 21). Nonhuman primate personality research would benefit from more consistency in methodology and instruments. Further development of chimpanzee personality instruments should include sufficient detail to provide scoring of facet-level equivalence.

At one level, each adjective used in the present study could be regarded as a trait. From the ratings on the adjectives, therefore, the highest five or seven trait scores could be used to describe each individual (these numbers suggested as providing definitive pictures of a human individual, e.g., Digman 1990). Thus, to contrast two

adult male chimpanzees, for example, we could describe Boris as *effective, popular, confident, curious, strong, paternal* and *intelligent*, whereas we would see that William is *deferential, fearful, gentle, apprehensive, strong, eccentric* and *excitable*. Beyond this level, however, it is evident that certain adjectives are highly intercorrelated and form trait clusters. Among chimpanzees, there are clusters relating to (1) confidence and status, (2) sociability and activity, (3) intelligence and opportunism, and (4) aggression and excitability (Murray 1995, 2002). Cluster (1) is evident for gorillas and bonobos as well, while cluster (2) is represented among bonobos as sociability and among gorillas as activity. Cluster (4) is very similar to the adjectives relating to aggression in gorillas and to protection and aggression in bonobos, while cluster (3) is matched in gorillas, but is not present among bonobos (Murray 1995). Of course, these clusters give a strong indication of likely underlying dimensions and, because the clusters are comparable across species, it is possible to calculate scores for the gorillas and bonobos based on standardized ratings of the individuals on selected adjectives from each of the components identified for the chimpanzees (Murray, in prep.).

The meaning of factors, or dimensions of personality, can be interpreted in different ways. Thus, the chimpanzees' factor scores taken as representing levels of Confidence, Sociability and Excitability may be regarded as central (Allport 1937) or source (Cattell 1946) traits of personality, which can characterize an individual.

A criticism of placing too much emphasis on factor scores is that specificity is sacrificed for the sake of generality (Buss 1989; John 1989; McAdams 1992). However, here I offer an elucidation of the relationships between overt behaviors and both overall personality factors and specific trait adjectives. Examination of how behaviors link to factor scores offers a quicker and more general "snapshot" picture while the relationships of behaviors to specific adjective ratings likely have greater power for providing richer detail because they are more discrete measurements. Therefore, Figs. 6.1–6.3 are diagrammatic representations of the predictive relationships between adjectives and behaviors, according to the underlying factors of personality. They provide a readily understood characterization of the chimpanzee personalities as they show relationships between the adjectives (narrower trait terms) and behaviors, within the overall dimensions of personality, rather than just between factor scores and behaviors.

Because all adjectives which had factor loadings above 0.317 are shown, some appear on more than one component; however, they are all presented so that each component and its relationships with the behavioral measures may be considered independently.

6.3.7.1 C1: Confident/Apprehensive

Figure 6.1 shows a clear delineation between adjectives loading highly positively on C1 and a subset of behaviors that correlate with those adjectives, and between adjectives loading highly negatively on this component and another distinct group of behaviors correlating with them. The predictive value of these relationships between

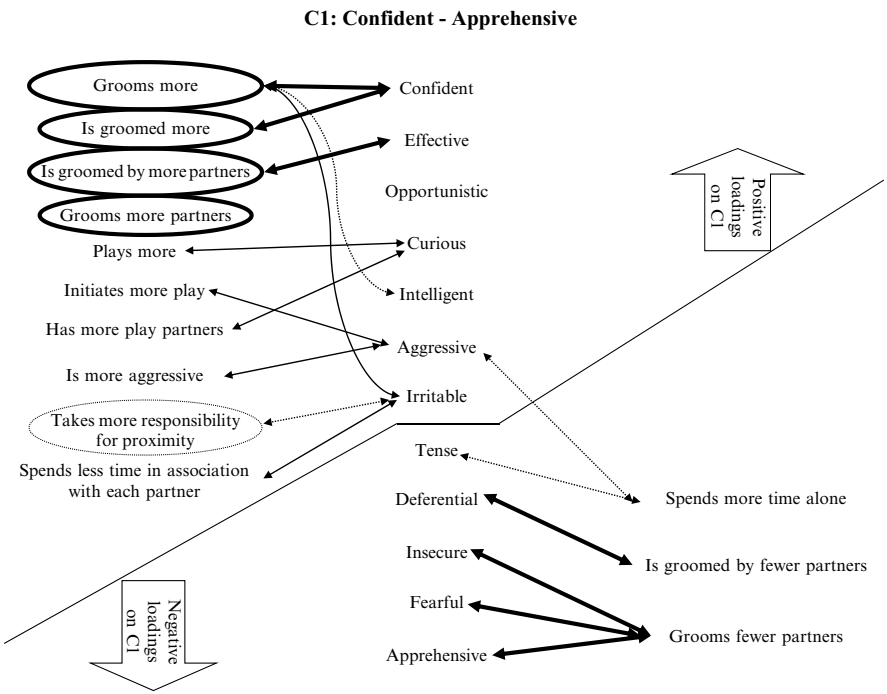


Fig. 6.1 Predictive relationships ($p < 0.001$) between adjectives loading on C1 (at 0.317 or more) and behaviors in chimpanzees. *Normal lines* = all chimpanzees; *bold* = relationships present only in males; *dotted* = relationships present only in immatures; *ovals* = behavior correlates with high scores on C1 ($p < 0.01$) in males (*bold*) or immatures (*dotted*) only

adjectives and behaviors is excellent as, with the exception of one relationship among immature chimpanzees, there is no overlap, i.e., none of the adjectives loading positively are positively related to what could be termed the “negative” behaviors (e.g., spending more time alone and/or not engaged in social behaviors). From Fig. 6.1, a high/low distinction can be made, whereby high ratings on the adjectives above the line, and/or high scores on C1 (which reflect high ratings on the positively loading adjectives and low ratings on the negatively loading adjectives) are related to more grooming, play and aggression, while high ratings on the adjectives below the line are related to less grooming and spending more time alone.

While such predictive power is encouraging, the relationships illustrated may not necessarily always hold. Caution should be exercised particularly when generalizing to other groups of individuals because, not only will the age or sex ratio of other groups vary, but so may other circumstances such as grouping, rearing history, and the experiences of the individuals. However, these diagrams also highlight which relationships are differentially found within a specific sex or age class. The relationships between increased grooming and the traits *confidence* and *effectiveness*, for example, are only evident among male chimpanzees. This is

important because it enables prediction among a specific group of individuals. Similarly, the finding that, among immature chimpanzees, more *tense* individuals spend more time alone, could be useful for animal caretakers when taken as an indication of tension within the group.

A relationship between grooming frequency and dominance rank in primates including chimpanzees and baboons has frequently been identified (Sparks 1969; Buirski et al. 1973; Simpson 1973; Seyfarth 1980; Schino 2001, 2007), with dominant animals grooming others less frequently, but receiving more grooming and deference themselves. However, correlations between grooming measures and Component 1, relating to confidence and effectiveness, are not entirely in accordance with this generalization. Specifically, male chimpanzees with high C1 scores groom more partners and are groomed by more partners, but they have higher rates of grooming. Vervet monkeys scoring highly on a status-linked factor termed Social Competence also engage in more grooming (McGuire et al. 1994). Male chimpanzees rated highly on *effective* are groomed by more partners, while more *confident* males receive more grooming.

The finding that immature chimpanzees rated as more *intelligent* engage in more grooming than their peers can be interpreted as supporting Goodall's (1986) view that lower status animals groom those with a higher rank than their own, using grooming as a strategy of manipulation and ingratiation. It can also be used as a method of appeasement, perhaps by an immature chimpanzee who has been punished by the alpha male for being too rough in play. It may also reflect an interchange relationship (Seyfarth and Cheney 1984; Cheney et al. 1986; Hemelrijk and Ek 1991), in which grooming is exchanged for coalitionary support in antagonistic encounters. These explanations in which grooming and support during aggression can be seen as reciprocally altruistic (Trivers 1971; Seyfarth and Cheney 1984; Hemelrijk 1994; Schino 2007) also attribute to individuals, including those that are young, the capability for future planning, in that they plan to develop affiliative relationships to obtain, maintain, or increase their social status.

6.3.7.2 C2: Sociable/Solitary

A clear high/low distinction is also evident between adjectives loading highly positively on C2 and an associated group of behaviors, and adjectives loading highly negatively on this component and another group of behaviors (Fig. 6.2). Individuals with high ratings on the adjectives above the line, or high scores on C2, are more likely to play more with more partners, solicit more grooming and spend less time alone. Those rated more highly on adjectives below the line, conversely, play less, spend more time alone, are aggressive, and display more. They also engage in more grooming. Males who are more playful and/or who have higher C2 scores are less likely to display frequently, while immatures scoring highly on C2 are less aggressive and receive more grooming from more partners.

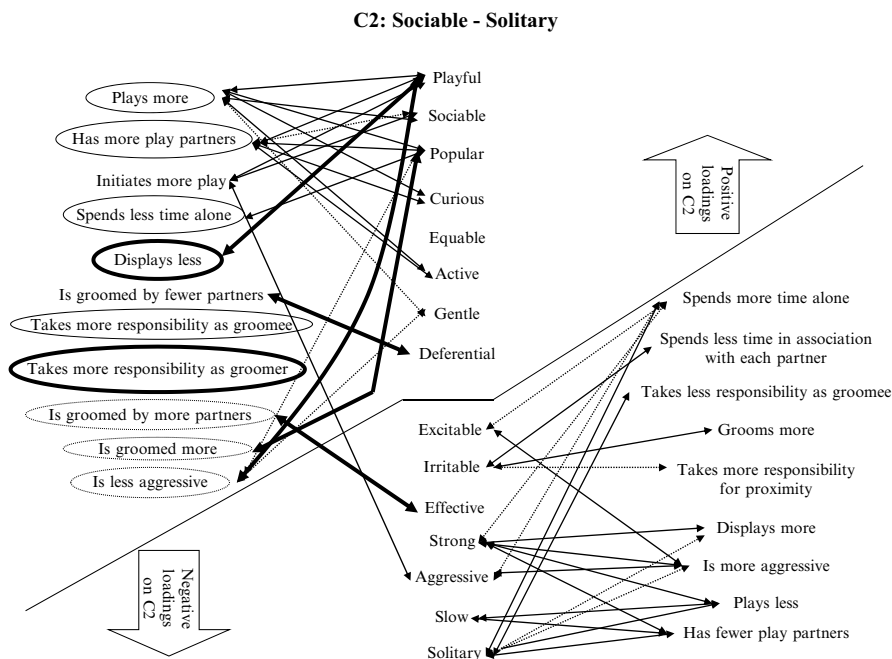


Fig. 6.2 Predictive relationships ($p < 0.001$) between adjectives loading on C2 (at 0.317 or more) and behaviors in chimpanzees. *Normal lines* = all chimpanzees; *bold* = relationships present only in males; *dotted* = relationships present only in immatures; *ovals* = behavior correlates with high scores on C2 ($p < 0.01$) in all chimpanzees (*normal lines*), in males (*bold*) or in immatures (*dotted*)

The findings that chimpanzees scoring highly on C2 spend less time alone and play more with more partners are in accordance with previous findings that vervet monkeys' scores on a Playful/Curious factor were positively related to play and negatively related to being solitary (McGuire et al. 1994). They also support the labeling of this C2 component as Sociable/Playful to Solitary (Murray 1995), since it has been argued that, rather than using factor loadings, factors should be identified from their correlations with external criteria (Kline 1992, 1993). In revisiting my earlier finding that more measures relating to play rather than to grooming correlate with sociability (Murray 2002, 2005), I categorized the chimpanzees as "unsociable," "sociable" or "very sociable" according to their scores on C2, and I also classified them in terms of levels of grooming and play behavior using sample median splits. I found that all unsociable chimpanzees are nonplayful, but nevertheless groom at medium and high rates; and most very sociable individuals are low groomers but classed as either playful or very playful. Binomial tests revealed no significant relationship between sociability categories and grooming, but nonplayful apes are more likely to be unsociable ($p < 0.001$) and playful apes significantly more likely to be very sociable ($p < 0.05$). Perhaps the best indicator for generalizing about how sociable individuals are therefore is their C2 score.

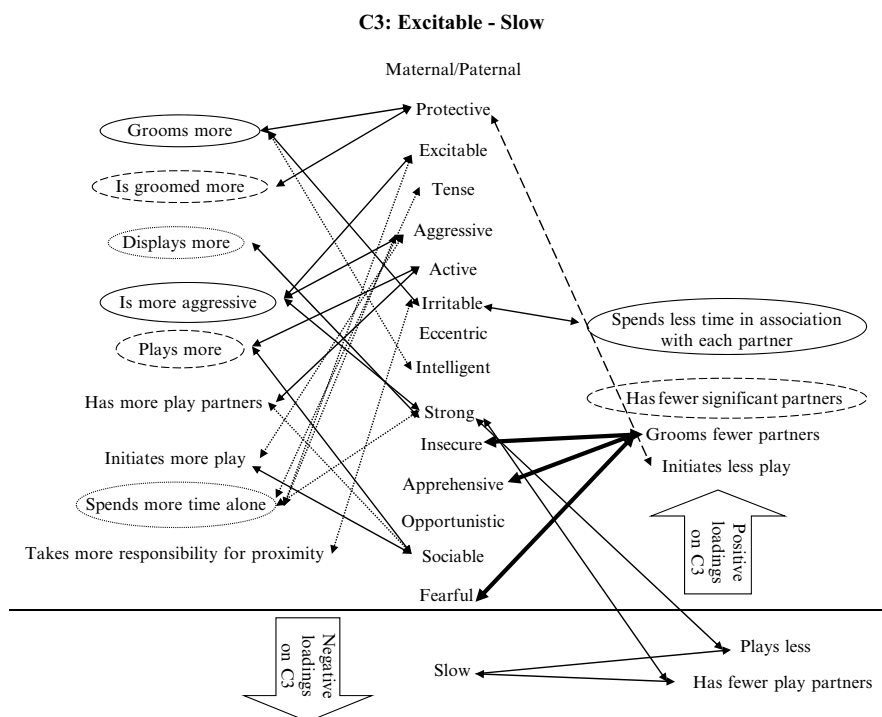


Fig. 6.3 Predictive relationships ($p < 0.001$) between adjectives loading on C3 (at 0.317 or more) and behaviors in chimpanzees. *Normal lines* = all chimpanzees; *bold* = relationships present only in males; *dotted* = relationships present only in immatures; *dashed* = relationships present only in adults; *ovals* = behavior correlates with high scores on C3 ($p < 0.01$) in males (*bold*) or immatures (*dotted*) only

6.3.7.3 C3: Excitable/Slow

Figure 6.3 shows that the “high/low” distinction on the third component is less clear-cut. All the adjectives above the line have high positive loadings on C3, while only one – *slow* – has a high negative loading. Chimpanzees with high ratings on *slow* play less. However, making predictions about the behavior of chimpanzees with high ratings on the other adjectives, or higher scores on C3, is more problematic. The behaviors relating to these adjectives can broadly be encompassed within the realms of more play, more grooming, and more aggression. Chimpanzees with high C3 scores groom more, but spend less time in association with each partner. Adults high on C3 play more and receive more grooming, although they have fewer partners overall. Immature chimpanzees scoring highly on C3 tend to spend more time alone and display more.

The trait *aggressive* loads most highly on C3, and individuals with high scores on this component also have higher rates of aggression. Ratings on the adjective *aggressive* are positively correlated with actual rates of aggression, and chimpanzees who display more are rated as *stronger*. Immature chimpanzees rated as more *aggressive* take more responsibility for initiating play, while immature chimpanzees rated as more *solitary* have higher rates of aggression and displays. Overt aggression is relatively rare in many groups of primates, e.g., olive baboons (*Papio anubis*: Buirski et al. 1973), although rivalry among male chimpanzees in captivity has resulted in the death of more than one male in multi-male groups (Wolfe, quoted in Goodall 1986, p. 419; de Waal 1986). In my study, such extreme aggression was not witnessed, and display rates were generally higher than rates of aggression. Nor were there many obvious cases of coalitions or alliances between individuals. Long-term stability in a group may reduce competition between males for females because the extended exposure to the same females by captive males may also reduce their sexual interest (Lambeth et al. 1990). The difference, therefore, between the Chester and Arnhem multi-male groups (see above: de Waal 1986) is hard to explain, but could be related to the stability of dominance relationships, which may act to constrain sexual and aggressive behavior. It could be that our increasing understanding of the relationships between personality and behavior will help us with just these sorts of questions, and can have implications for the welfare and well-being of animals.

6.4 Conclusions

The thrust of traditional trait theories (Allport 1937; Cattell 1973) is that traits determine behavior, with the reciprocal influence of behavior and learning back to traits being minimal. According to this directionality, *confident* male chimpanzees, for example, will groom more than those who are less confident; but the fact that an individual male grooms a great deal does not necessarily mean that he is more confident than others. This should be kept in mind when interpreting the information contained in Figs. 6.1–6.3, although their utility is likely to be in the direction of predicting from trait to behavior.

Measuring personality and being cognizant of how it can affect behavior has important applications for animal welfare. Certain personality profiles may be more suited for particular roles, for example, adopting an orphan (van Wulfften Palthe and van Hooff 1975; Holzer Blersch and Schmidt 1992), whereas others may warn of potential friction within a group by identifying potential negative reactions to the proposed introduction of a newcomer. Watts (1994), for example, found that female gorillas who were long-term residents within a stable group were relatively intolerant of immigrants, and that this intolerance persisted even after 2–3 years. The Confident, Sociable and Excitable factor scores of individuals, their personality

types, or mean ratings on particular adjectives, can be used for selection of individuals for different purposes. To select the best first candidate to introduce to a hand-reared infant about to be integrated into an established group, for example, one might look for an individual with a relatively high Sociable score, but perhaps a mid-range score on Confident and Excitable, and with high ratings on the adjectives *maternal/paternal*, *equable*, and *gentle*. Selection according to personality profiles has also been suggested for managers of the Gorilla Species Survival Plan (Gold and Maple 1994). Desiring a “good candidate” for a bachelor group, for instance, Gold and Maple recommend looking for a male with a relatively high Extraverted score and a comparatively low Dominant score. Kuhar et al. (2006) also report that in the two known cases thus far of a juvenile male gorilla being introduced to a silverback for the purposes of forming a multi-male group, those silverbacks scored almost two standard deviations above the mean on the factor Understanding, which Kuhar et al. have identified as the most relevant (thus far) in giving an indication of individuals less likely to engage in noncontact aggression. Some of the links found here between personality and behavior might also be useful for captive management and conservation; for example, more tense immature chimpanzees spend more time alone and therefore groups in which chimpanzees spend more time alone may indicate group tension.

Many areas of psychological life are encompassed by the term *personality* in addition to interactions in the social arena. Varied aspects of the individual, such as emotion, motivation, attitudes, cognition, learning and arguably intelligence are incorporated in a description of personality (Cervone and Pervin 2008). We will probably always struggle to know for certain what an animal subjectively or consciously experiences just by observation and psychological researchers may wish for some way to ask subjects about themselves. Perhaps the language apes may yet provide another dimension to our information on such subjective topics. It is possible, however, that the taxonomy provided by models such as the FFM may be inadequate for personality description by these apes themselves, and their vocabulary and context usage will obviously be influenced by the humans who teach them.

An alternative methodology for studying personality in nonhumans is not likely to readily become available. The trait approach offers us many insights into understanding closely related species, but caveats should always be borne in mind. One of the most extreme criticisms of factor models of personality argues that they offer little more than an envisaged very broad description of how human beings might be described to aliens (McAdams 1992). It is possible that critics would extend this view to the utilization of factor scores from similar instruments used to measure personality in nonhumans. Ratings are similarly criticized as limited by the omission of any context, such that the whole exercise deteriorates to the point where the aim is merely to “...get a general, superficial, and virtually nonconditional picture of ... personality.” (McAdams 1992, p. 350). However, the rating

scale method, as applied to the apes in this study, can provide both a description of the overall pattern of an individual's behavior in terms of factor scores (in contrast to a possible myriad of pure measurements of more discrete events, which might not enable a clear "picture" of individuality), yet also yield more detailed information at the adjective trait level. Furthermore, although the factors that emerged as quantifiable for these apes are similar to those found for other ape and monkey species, the range of variation or strength of manifestation of those personality domains may not be, and the traits are not necessarily semantically identical across species.

How individuals resemble and differ from each other in terms of their personalities and overt behaviors are some of the most interesting problems that can be tackled. In this chapter, I have reviewed studies providing validation of personality trait ratings and factors. A picture is steadily building to inform us about links between the behaviors we observe in primates and their "inner world" of individuality. In addition to relationships between discrete trait ratings and overt behaviors, I have demonstrated links between more global scores on major underlying personality factors and behaviors, and I have shown that some behaviors are differentially related in males/females and immatures/adults to personality traits and factors.

From the phylogenetic perspective, the net should be cast wider now to include New World monkeys and to consolidate and broaden findings on the Old World monkeys and apes, especially in relation to personality–behavior relationships on multi-faceted levels. This may yield important information on the evolution of personality structure and its relation to behavior. We also need studies in the wild to confirm the constancy and species-specificity of personality and its links to behavior. While there is growing support for the generality of chimpanzee personality across different captive settings, including zoos and a sanctuary (King et al. 2005), it is possible that the relationships between personality variables and behavioral manifestations may yet be quite different given such diverse situational and experiential contexts. King and Weiss (2011) point out that personality data from the wild is virtually nonexistent, despite many long-term behavioral studies which could easily incorporate it as a variable. One would suspect the case to be very different with captive studies; yet the difference is in fact not so profound, with a relative paucity of studies addressing how personality and behavior relate. I echo the call of others to include personality measurement alongside other ongoing research and to standardize the methodology for greater comparability – and more intriguing insights into primate personality.

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Appendix 1 Chimpanzee personality factors derived via principal-components analysis

C1	23.70%	C2	18.40%	C3	15.40%	C4	9.30%	C5	5.70%	C6	5.10%
Confident	0.924	Playful	0.829	Mat./Paternal	0.689	Gentle	0.822	Intelligent	0.637	Solitary	0.392
Effective	0.730	Sociable	0.737	Protective	0.604	Equable	0.645	Opportunistic	0.412	Strong	0.327
Opportunistic	0.588	Popular	0.692	Excitable	0.598	Slow	0.554	Slow	0.296	Eccentric	0.325
Curious	0.521	Curious	0.535	Tense	0.567	Protective	0.484	Curious	0.224	Curious	0.293
Intelligent	0.470	Equable	0.421	Aggressive	0.516	Mat./Paternal	0.462	Deferential	0.158	Equable	0.259
Aggressive	0.440	Active	0.374	Active	0.495	Popular	0.214	Mat./Paternal	0.157	Deferential	0.228
Irritable	0.337	Gentle	0.355	Irritable	0.486	Effective	0.184	Apprehensive	0.138	Active	0.210
Popular	0.292	Deferential	0.349	Eccentric	0.470	Solitary	0.168	Protective	0.109	Opportunistic	0.166
Active	0.279	Fearful	0.264	Intelligent	0.405	Eccentric	0.154	Tense	0.102	Intelligent	0.151
Sociable	0.237	Mat./Paternal	0.139	Strong	0.384	Deferential	0.119	Fearful	0.067	Tense	0.142
Strong	0.233	Insecure	0.094	Insecure	0.364	Strong	0.102	Irritable	0.062	Apprehensive	0.129
Protective	0.215	Opportunistic	0.082	Apprehensive	0.363	Confident	0.044	Insecure	0.022	Effective	0.073
Mat./Paternal	0.196	Intelligent	-0.010	Opportunistic	0.353	Intelligent	0.043	Sociable	0.020	Playful	0.023
Equable	0.194	Confident	-0.017	Sociable	0.351	Apprehensive	0.037	Solitary	0.000	Protective	0.021
Playful	0.147	Apprehensive	-0.041	Fearful	0.335	Excitable	0.003	Aggressive	-0.073	Confident	-0.062
Slow	0.067	Eccentric	-0.146	Playful	0.276	Curious	-0.010	Confident	-0.096	Aggressive	-0.066
Solitary	-0.202	Protective	-0.172	Deferential	0.240	Insecure	-0.023	Playful	-0.098	Sociable	-0.095
Excitable	-0.223	Tense	-0.224	Effective	0.233	Sociable	-0.029	Equable	-0.124	Insecure	-0.119
Gentle	-0.225	Excitable	-0.358	Curious	0.212	Fearful	-0.052	Gentle	-0.154	Gentle	-0.124
Eccentric	-0.228	Irritable	-0.366	Popular	0.161	Tense	-0.100	Effective	-0.209	Popular	-0.134
Tense	-0.633	Effective	-0.458	Solitary	0.073	Irritable	-0.103	Excitable	-0.276	Slow	-0.157
Deferential	-0.721	Strong	-0.487	Gentle	0.021	Playful	-0.156	Active	-0.288	Fearful	-0.173
Insecure	-0.752	Aggressive	-0.504	Confident	-0.046	Opportunistic	-0.165	Popular	-0.296	Mat./Paternal	-0.229
Fearful	-0.759	Slow	-0.506	Equable	-0.200	Aggressive	-0.237	Eccentric	-0.325	Excitable	-0.355
Apprehensive	-0.850	Solitary	-0.784	Slow	-0.332	Active	-0.416	Strong	-0.375	Irritable	-0.516

Personality Rating Scale (Murray, 1995, adapted from Stevenson-Hinde & Zunz, 1978)

-
1. **Active** - moves about a lot.
 2. **Aggressive** - causes harm or potential harm.
 3. **Apprehensive** - seems to be anxious about everything; fears and avoids any kind of risk.
 4. **Confident** - behaves in a positive, assured manner; not restrained or tentative.
 5. **Curious** - readily explores new situations.
 6. **Deferential** - gives in readily to others.
 7. **Eccentric** - shows stereotypes or unusual mannerisms.
 8. **Effective** - gets own way; can control others; leads.
 9. **Equable** - reacts to others in an even calm way; is not easily disturbed.
 10. **Excitable** - over-reacts to any change.
 11. **Fearful** - fear-grins; retreats readily from others or from outside disturbances.
 12. **Gentle** - responds to others in an easy kind manner.
 13. **Insecure** - hesitates to act alone; seeks reassurance from others.
 14. **Intelligent** - clever; tactical; manipulative; inventive.
 15. **Irritable** - reacts negatively with little provocation.
 16. **Maternal/Paternal** - warm and receptive to infants.
 17. **Opportunistic** - seizes a chance as soon as it arises.
 18. **Permissive*** - could, but does not, interfere with the behaviour of others.
 19. **Playful** - initiates play and joins in when play is solicited.
 20. **Popular** - is sought out as a companion by others.
 21. **Predictable*** - consistent in behaviour.
 22. **Protective** - prevents harm or possible harm to others.
 23. **Sensitive*** - responds or reacts with minimal cues to the behaviour of others.
 24. **Slow** - moves and sits in a relaxed manner; moves slowly and deliberately; not easily hurried.
 25. **Sociable** - seeks companionship of others.
 26. **Solitary** - spends time alone.
 27. **Strong** - depends upon sturdiness and muscular strength.
 28. **Tense** - shows restraint in posture and movement.
-

*Adjectives subsequently omitted from analysis due to poor intra-item reliability.

Instructions to raters for completing the personality ratings

Ratings must be made independently without discussion with other raters. The ratings should be made on the basis of your knowledge of the individual animals within the last month and should be completed as soon as possible. If there is any reason why the behaviour of the animals is not typical of any other period of time, please feel free to comment on this on a separate sheet of paper. For each animal, please rate each item in turn, independently, and according to its definition. For each

item, place a circle around the number which you feel best illustrates the strength of the particular behaviour in each individual:

1. None of the behaviour
2. Traces of the behaviour present
3. Behaviour distinctly present, but a little less than average
4. Average, or slightly above average
5. Strong, but not outstanding, evidence of the behaviour
6. Strong and conspicuous behaviour, approaching the extreme
7. Extreme manifestation of the behaviour

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